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Review

Interaction of plant growth promoting bacteria with tomato under abiotic stress: A review

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ABSTRACT

Tomato is one of the most demanding/utilizable vegetable crops worldwide after potato. It is extensively cultivated throughout the tropics and sub-tropics around the world. However, certain climate change consequences like salinity, drought, and environmental pollutants particularly heavy metals etc., lead to low soil productivity. In fact, problem of salinity, drought and soil contamination are increasing rapidly throughout the globe and severely affecting more than 10% of arable land resulting into reduction of more than 50% average yields of major crops including tomato. Therefore, sustainable agriculture is in great demand under current alarming condition of food security. Plant growth promoting bacteria (PGPB) has been evident as a co-evolution between plants and microbes showing antagonistic and synergistic interactions. Therefore, utilization of PGPB to tackle the problem of salinity, drought and heavy metal contamination is one of the novel biological approaches for sustainable agriculture practices. Under stress conditions, plant hormone like ethylene is known to endogenously regulate the homeostasis of plants leading to significant reduction in root and shoot growth. Few PGPB like *Pseudomonas* sp. and *Bacillus* sp. have developed tolerance mechanism against varieties of heavy metals through mobilization, surface complexation, biosorption, precipitation, intracellular compartmentalization or immobilization processes. Looking into the multiple applications of PGPB in sustainable agriculture, scientists and policy makers are currently emphasizing over selection of suitable microbial communities through interdisciplinary research disciplines including agriculture, biotechnology, chemical engineering, environmental science and nanotechnology to bring together different ecological and functional biological approaches to provide new formulations and opportunities with immense potential. The present review entails the overview of current trends in PGPB mediated abiotic stress amelioration in order to encounter the negative impacts of changing climatic conditions for sustainable enhancement in tomato productivity.

1. Introduction

Tomato (*Solanum lycopersicum* L.) is the world's most cultivated solanaceous vegetable crop next to potato (Pedro and Ferreira, 2005). In 2013, global production of tomato was approximately 164 million tones which cover an area of 4.8 million hectares with 7th rank in productivity (FAOSTAT, 2013; Luna et al., 2016). Currently, more than 3000 species of tomato are reported worldwide. *Solanum lycopersicum* (L.) is the most common species in its occurrence and domestication. The tomato can be consumed in raw as well as in industrially processed form like pulp and sauces. Tomato is considered as a good source of dietary minerals, vitamins (vitamins C and E), lycopene (80%), folic acid, flavonoids, β-carotene and potassium ions (Willcox et al., 2003). In addition, few organic acids of nutritional importance like (malic acid, ascorbic acid, citric acid) and trace elements (such as iron, zinc, copper, calcium, potassium and magnesium) are also reported as essential ingredients of tomato.

Tomato contains different types of pigments including lycopene (a non-provitamin A), one of the major constituents responsible for remarkable antioxidant activity that helps in reduction of risks of cancer and heart diseases (Rao and Agarwal, 1999). Most of the lycopene content in food items is derived from tomato followed by other sources like watermelon, guava and pink grape fruit (Lin and Chen, 2003; Levy and Sharoni, 2004). Currently, worldwide productivity of tomato is facing the challenges of biotic and abiotic stress factors. Drought and salinity are the two leading environmental stresses in agriculture that limits the global productivity of major crops directly by reducing the growth and yields (Cuartero et al., 2006; Nuruddin et al., 2003; Kaushal

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and Wani, 2016a,b). Apart from these stresses, presence of toxic heavy metals and/or metalloids in the agro-ecosystem is also one of the important factors limiting the crop productivity (Oztürk, 2007). Rapid industrialization and population expansion are the major factors responsible for generation of enormous amount of toxic and hazardous metals in soil environment of both developed and developing countries. Soil acts as the major sink for different heavy metals including Fe, Mn, Pb, Cd, and Cr. Heavy metals in environment are released by natural (geogenic) as well as anthropogenic activities (wastewater irrigation, industrial effluents, chemical pesticides). Unlike organic contaminants, heavy metals do not undergo microbial or chemical degradation (Kirpichtchikova et al., 2006), rendering their long term persistence in soil environment (Adriano, 2003). Large amount discharge of noxious heavy metals into agricultural fields causes metal accumulation thus, food chain contamination (Costa and Duta, 2001) beyond the prescribed safety limits in cultivated crops causing hazardous impact on human health (Li et al., 2006).

It is well known that high concentration of different heavy metals affects the natural environments and human beings directly or indirectly through various ways (Srivastava et al., 2012; Wilson and Pyatt, 2007). Growth and yield of plant is severely affected by high content of soil heavy metals, resulting from application of various fertilizers, pesticides, irrigation with sewage water and sludge addition in cultivable fields (Frost and Ketchum, 2000). Contamination of heavy metals in soil depends on quantity and nature of pesticides used in soil, level of emission and transport of heavy metals from nearby sources including industries and mining sites. Micronutrients like Mn, Fe, Zn, Cu, Ni and Co are essential for growth of plants, animals and microorganisms in low concentrations, while elements like Cd, Hg and Pb have no essential role in the vital biological activities (Ali et al., 2013). Being highly toxic even at very low concentrations (Gadd, 1992), the elevated concentration of such metals above threshold levels in soils as well as the long term persistence of potentially toxic heavy metals (e.g., Cd and Pb) and metalloids (e.g., As) in agricultural field may adversely influence the physico-chemical and biological properties of soil in a quantitative as well as qualitative manner (Ahemad, 2012, 2014).

In addition, presence of xenobiotics such as organic compounds particularly polycyclic aromatic hydrocarbons (PAHs) have long been reported to pose threat to agro-ecosystems thus, severely affecting the crop plant productivity as well as human health (Fine et al., 1997; Overcash and Pal, 1979). The PAHs are a group of complex organic chemicals having more than hundred different organic compounds which are generated by incomplete combustion of organic matters, forest fires, traffic, household heating and waste incineration (Johnsen et al., 2005). Their wide distribution and long term persistence in soil and water environment largely depends on physical and chemical characteristics of PAHs.

Application of plant growth promoting bacteria (PGPB) to alleviate the negative impacts of environmental stresses is a cost effective and eco-friendly biological approach as compared to physico-chemical methodologies currently being applied. During last two decades, many research groups have broadly used PGPB strains to enhance growth and yields of plants under environmental stress (Bacilio et al., 2004; Sessitsch et al., 2013; Kumar et al., 2014; Ji et al., 2014; Mayak et al., 2004a, b; Rolli et al., 2015; Timmusk et al., 2015; Zahid et al., 2015). Besides stress management, PGPB also serve as biocontrol, bio-fertilizer or phyto-stimulator, which helps in soil fertility maintenance by removing heavy metals and other soil contaminants, thereby acting as a promising alternative to indiscriminately used hazardous chemical fertilizers for sustainable agriculture (Fig. 1) (Kloepper et al., 2004a,b; Glick, 2014; Majeed et al., 2015; Singh et al., 2017a,b; Dal Cortivo et al., 2017). Therefore, in present review we have attempted to provide an overview of role of PGPB in abiotic stress amelioration for enhanced tomato productivity.

2. Role of plant growth promoting bacteria (PGPB) in plant growth and development

Term rhizosphere designates to plant roots and surrounding soil (a thin layer of soil adhered to the plant root surface) and is the most prominent zone responsible for diverse microbial interactions (Kumar et al., 2015). Various level of interactions are favored by plant's root due to synthesis and secretion of large amount of carbohydrates, lipids, organic acids, and amino acids as root exudates favoring the interaction of diverse microbial communities in rhizosphere which facilitates effective microbial colonization (Brimecombe et al., 2007; Oku et al., 2012; Kumar et al., 2015). Root exudates of tomato includes various biochemical components like amino acids (glutamic acid, aspartic acid, leucine, isoleucine, and lysine), organic acids (citric acid, malic acid, and succinic acid), and sugars (glucose, xylose) (Kamilova et al., 2006; Oku et al., 2012; Singh et al., 2017a,b). The components of root exudates are known to effectively participate in microbial colonization of tomato root and essentially involved in biocontrol of root pathogens (Suslow et al., 1982). Plant growth in soil environment is markedly influenced by many abiotic and biotic factors including microbes (Singh, 2015). Bacteria are the most abundant group of microorganisms coexisting with fungi, actinomycetes, protozoa and algae in the rhizosphere. Due to dominance of bacterial population in the rhizosphere, their influence on plant physiological processes is highly anticipated (Barriuso et al., 2008). Hayat et al. (2010) reported that the rhizospheric bacteria are the most versatile in transforming, mobilizing, and solubilizing the nutrients compared to bulk soils. Microorganisms colonizing the rhizosphere can be classified according to type of interactions with plants; some may act as pathogens, whereas others may trigger beneficial interactions such as growth promotion and metabolite synthesis in host plants (Kumar et al., 2017a,b). In past decades, exploration and identification of PGPB attributes (siderophore production, antibiotic production, biocontrol, etc.) have received tremendous momentum because of their participation and contribution in the rhizosphere functions (plant growth promotion, bio-geochemical cycling, plant protection against pathogens, etc.). Some of the outstanding examples of plant growth promoting bacteria (PGPB) are *Alcaligenes*, *Arthrobacter*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Klebsiella*, and *Pseudomonas* (Mellado et al., 2007; Lee et al., 2016; Hammami et al., 2013). These PGPBs have been employed as plant or soil inoculants for growth promotion and yield enhancement in plants as well as to maintain soil productivity and nutrient availability.

3. PGPB mediated growth and yield enhancement in tomato

Plant growth promoting bacteria (PGPB) are one of the most promising organisms for growth and yield enhancement in different plants species including tomato. Ribaudo et al. (2006) reported beneficial interaction of *Azospirillum brasilens* FT326 with tomato plants. Tomato seed inoculation with nitrogen fixing *Azospirillum brasilens* FT326 was observed to significantly enhance the root and shoot weight as well as length of root hairs, which may be due to higher amount secretions of important phytohormone *i.e.* indole-3-acetic acid (IAA) and ethylene. Surface bacterization of tomato, groundnut, sorghum and chickpea with the bacteria (isolated from rhizoplane, rhizosphere and phylloplane region of tomato) resulted into positive growth response only in case of tomato while neutral or negative effects were observed for groundnut, sorghum and chickpea. The study concluded that bacteria with plant growth promoting traits did not positively influence the growth of all selected plants; they may perform host specificity (Vaikuntapu et al., 2014). Other researchers have also reported the similar plant growth promoting effect induced by well known PGPB *Pseudomonas fluorescens* (Gupta et al., 2015). Under green house conditions, different PGPB combinations were found to pose different effects. Increase in root and shoot weight with increased absorption of mineral elements like N, P, K, Ca and Mg were noticed under altered

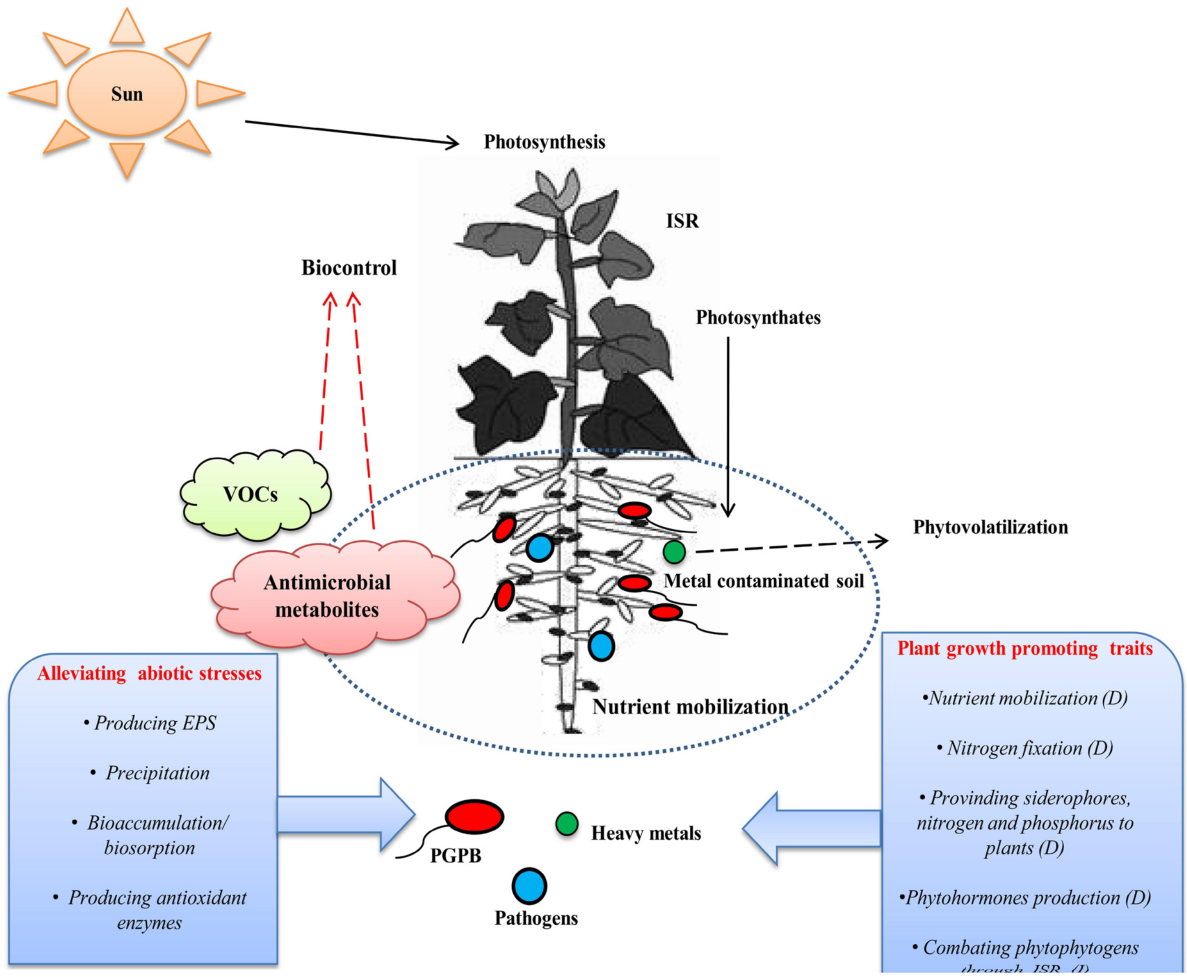

Fig. 1. An overview of diversified PGPB traits that affect the plant growth directly or indirectly. Direct roles include, nutrient mobilization, nitrogen fixation, phytohormones productions. Indirect roles involve growth inhibition of phytopathogenes through induced systemic resistance, antimicrobial metabolites, etc. In addition, PGPB protect plants from various abiotic stresses, such as salinity and drought through exopolysaccharides (EPS) and antioxidant enzymes. Tolerance against heavy metals is rendered through precipitation, surface complexation, bioaccumulation or biosorption.

treatment of single and combined dose of bacterial strains. Maximum absorption of N, P, and K was recorded for tomato treatments receiving combination of *Pseudomonas*, *Azotobacter*, and *Azospirillum*. Shen et al. (2012) examined the effect of PGPB (*Erwinia persicinus* RA2, *Bacillus pumilus* WP8 and *Pseudomonas putida* RBP1) with and without ACC deaminase activity on growth and yield of tomato. *Erwinia persicinus* RA2 was proved to be the best suited PGPB for the enhancement of fresh and dry fruit weight of tomato as compared to others. Additionally, plants with PGPB treatment exhibited higher accumulation of sodium in leaves under salinity stress as compared to control, thereby making the plants salt tolerant. Almaghrabi et al. (2013) studied the effect of inoculation of six different isolates (*Pseudomonas putida*, *Pseudomonas fluorescens*, *Serratia marcescens*, *Bacillus amyloliquefaciens*, *Bacillus subtilis* and *Bacillus cereus*) on growth and yield of tomato. Plants treated with different bacterial species showed significant differences in plant height and shoot dry weight as compared to the untreated plants. Another green house study conducted by Lee et al. (2008) reported yield enhancement and significant increase in shoot length in tomato after 8 weeks of treatment with PGPB *i.e.* non purple sulfur bacteria. The PGPB treatment is also an attractive and environment friendly choice because it did not modulate the native bacterial community as evident by 16S rRNA denaturing gradient gel electrophoresis (DGGE). Koh and Song (2007) analyzed the impact of *Rhodopseudomonas* inoculation on seed germination and productivity of tomato and observed that the production of IAA (Indole-3-Acetic Acid) and ALA (5-Aminolevulinic Acid) was the main factor responsible for plant growth promotion. The bacterial inoculation may serve as effective biofertilizer for enhancement of crop productivity. Treatment with PGPB (either in single or combination) not only positively affected the plant growth as compared to control but also enhanced the uptake of nitrogen and phosphorus together with the increased activity of alkaline phosphatases. Furthermore, synergistic interaction of mycorrhiza and PGPB also accounted for the enhancement of microbial biomass carbon.

Effect of PGPB inoculation on growth and yield of hydroponically grown tomato was evaluated by Gravel et al. (2007). They found that treatment with *Pseudomonas putida* and *Trichoderma atroviride* under organic medium enhanced the fresh weight of root and shoot, as well as growth and yield of tomato by production of IAA, which was stimulated by addition of tryptophan, tryptamine and tryptophol. Treatment with *Pseudomonas* and *Trichoderma* were also reported to be efficient in minimizing the deleterious effect associated with exogenous IAA application. Violante and Olalde-Portugal (2007) investigated the effect of root application of *Bacillus subtilis* BEB-lSbs (BS13) on fruit quality such as size and texture of tomato and observed significant increase in yield of fruit, yield per plant and plant length in PBPB inoculated tomato than control. Tomato seeds treated with pink pigmented facultative methylotrophic bacteria (PPFMs) *Methylobacterium species* strain CBMB 20 and CBMB 10 demonstrated significant improvement in root length and accumulation of phytohormone *i.e.* cytokinin in extract (Ryu et al.,

2006). In another study, Gül et al. (2008) used open/closed nutrient system, nutrient concentration and PGPB inoculation to observe their effect on productivity of tomato. In open system, inoculation with plant growth promoting bacteria *Bacillus amyloliquefaciens* strain in spring season under hydroponic cultivation system of tomato enhanced the yield by 8–9 percent whereas negative impact on tomato yield was observed for closed cultivation system having half nutrient supplementation. In addition, molecular level changes in tomato treated with *Bacillus subtilis* is reported by Ongena et al. (2005) which involves significant changes in gene transcription as revealed by cDNA-AFLP analysis.

4. Role of PGPB in induced systemic tolerance (IST) in tomato against abiotic stress

Drought, salinity and contamination of heavy metals in soil are the major environmental stresses, causing alterations in physiological, biochemical and molecular processes of plants by exerting osmotic, oxidative as well as ionic stresses (Kaushal and Wani, 2016b). Plant root system is a primary factor which is influenced by different kinds of abiotic stresses such as salinity, drought, and soil heavy metals contamination. The interactions of microbes with crop plants play a prominent role in adaptation, maintenance and survival of both the partners in a number of abiotic stresses (Fig. 2). Induced Systemic Tolerance (IST) is the term used for PGPB mediated induction of abiotic stress responses. During last few decades the role of microbes in mitigation of abiotic stresses in plants has been the area of great attention for plant biologists and microbiologists (Nadeem et al., 2014; Souza et al., 2015). The intrinsic metabolic and genetic potential of several microbes helps to tolerate and alleviate negative impact of abiotic stresses in plants (Table 1). During salt stress management, PGPB activate plant antioxidant defense machinery by regulating the activity of superoxide dismutase (SOD), catalase and peroxidase, the key enzymes that scavenges over produced reactive oxygen species (ROS) (Jha and Subramanian, 2014; Islam et al., 2015). Under drought stress, certain glycine betaine producing or osmotolerant bacteria act synergistically with plant produced glycine betaine, and thus enhance the drought tolerance potential of plants (Dimkpa et al., 2009). Rhizobacteria also confer drought tolerance by regulating the levels of proteins, polysaccharides and important phytohormones. Therefore, the selection of stress tolerant microorganisms is of utmost importance to overcome the reduction and loss of growth and productivity of crop plants in stress affected areas. Therefore, field based experiments are currently being carried out in order to augment the PGPB mediated salinity and drought tolerance in tomato.

4.1. Salinity

Salinity is one of the most severe environmental stresses in current scenario that causes imbalance and reduction in growth and productivity of crops cultivated in arid and semi arid regions (Cicek and Cakirlar, 2002). Globally, huge areas of saline lands are reported which severely affects the nutrient status of soil and crop productivity. Therefore, to enhance the global crop productivity, it is very important to work on biological means of salinity stress mitigation. Use of PGPB is a safe and eco-friendly choice for environmental management and better agricultural practices. Several important aspects of plant metabolism are adversely affected by the level of soil salinity which results

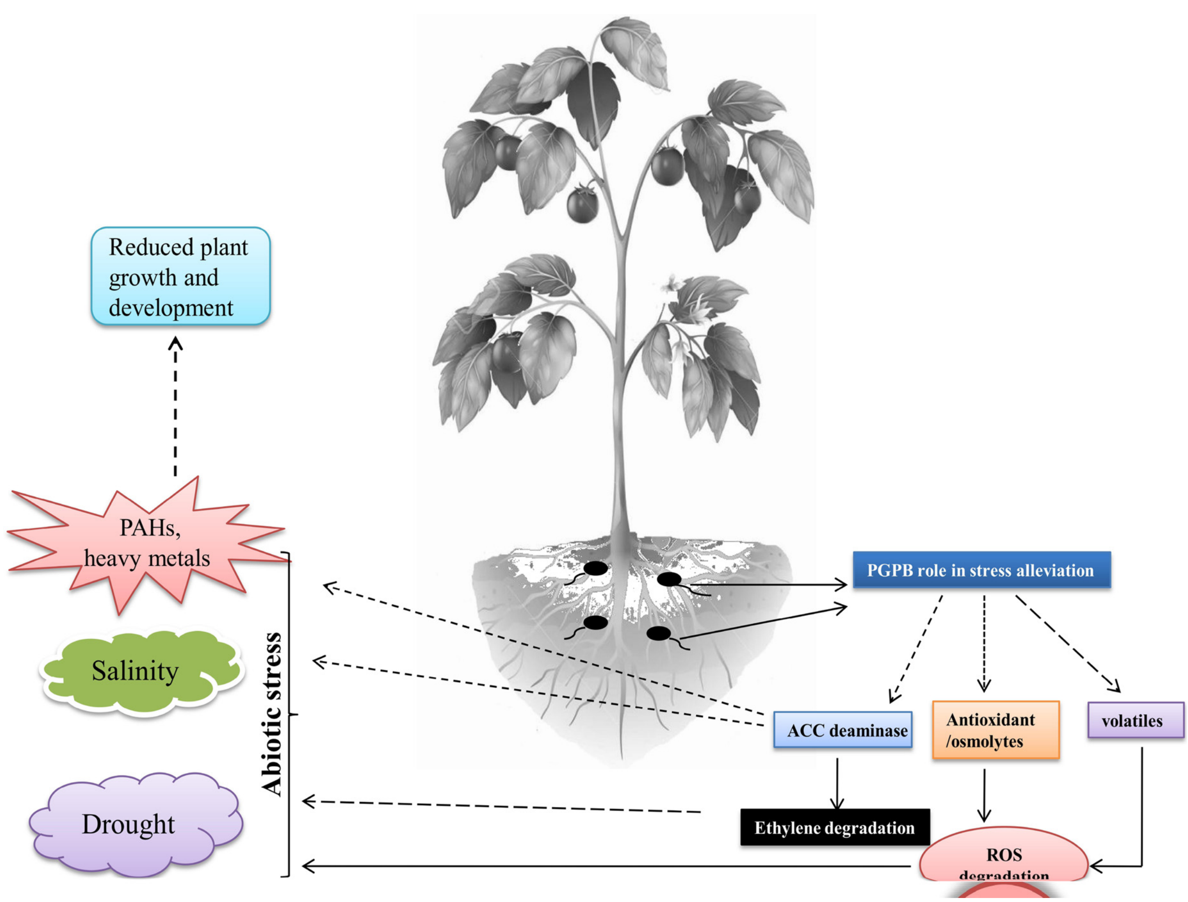

Fig. 2. PGPB mediated IST mechanisms against abiotic stress *i.e.* drought, salinity and heavy metals. ACC deaminase production by PGPB reduces ethylene concentration and helps plants to rescue the drought and salt stresses. Certain rhizosphere associated PGPB produces antioxidants and volatiles that results in significant degradation of ROS.

Table 1
Various abiotic stresses, their constraints and effective PGPB strategies.

Stress	Constraint	PGPB strategies	References
Salinity	Elevated salt levels (for example, NaCl) cause ion cytotoxicity and reduce osmotic potential	Increased accumulation of proline; decreased root and shoot Na^+ accumulation and enhanced root K^+ concentrations; SA-dependent pathway; expression of salt stress-related RAB18 plant gene	Barka et al. (2006); Sannazzaro et al. (2006); Barriuso et al. (2008); Jha and Subramanian (2014)
Drought	Low water potential	Increased photosynthesis, root and shoot biomass under drought conditions; defense related proteins and enzymes, antioxidants and epoxypolysaccharides; stress related genes and proteins; production of volatile compounds	Dimkpa et al. (2009); Nadeem et al. (2014); Timmusk et al. (2015); Lim and Kim (2013)
Metal stress/ xenobiotic compounds	Cytotoxicity; Production of ROS; Deposition of excess metal in vacuoles; Bioaccumulation; Protein damages	Siderophore production, ACC deaminase activity; increased soil dehydrogenase, phosphatase and available phosphorus; microbial colonization; volatilization	Dimkpa et al. (2009); Srivastava et al. (2012); Bisht et al. (2015)

Table 2
An overview of PGPB mediated salt tolerance mechanism in tomato.

PGPB and isolation sources	Experiments	Results	References
A. piechaudii ARV8; Southern Israel	Pot experiment; isolation and molecular characterization using 16S rRNA; ethylene production analysis; RWC and WUE observation	Bacterium reduced ethylene production and increases WUE indicating NaCl stress enhanced ethylene production	Mayak et al. (2004a)
PGPB isolated from rhizosphere of tomato; Gujrat, India	Pot experiment; PGPB isolation; ACC deaminase and siderophore production and phosphate solubilization; root and shoot parameters analysis	C4 and T15 PGPB isolates were the best growth promoters under 2% NaCl stress condition; however, C5 enhanced biomass production in tomato plants with increased uptake of the salts by plants, thereby reducing the salt concentration in the soil	Tank and Saraf (2010)
P. fluorescens YsS6 and *P. migulae* 8R6 isolated from rhizosphere of tomato; France and Canada, respectively	Pot experiment; endophytes isolation and characterization; root elongation assay; salt ion content estimation;	Plants treated with ACC deaminase producing wild type strains were healthier and grew to a much larger size under high salinity stress compared to plants pretreated with the ACC deaminase deficient mutants or no bacterial treatment	Ali et al. (2014)
Pseudomonas putida UW4; rhizosphere of reeds; Waterloo, Ontario	Pot experiment; plant growth analysis; chlorophyll content; q-PCR for Toc GTPases expression	PGPB significantly increased shoot length, shoot fresh and dry mass, and the chlorophyll concentration of tomato seedlings under stress condition; upregulated expression of Toc GTPase gene may facilitates the import into chloroplasts of proteins that are involved in the stress response	Yan et al. (2014)
PGPB isolates	Pot experiment; root and shoot morphology analysis; chlorophyll and carotenoid estimation; micronutrient content analysis in root and shoot; enzymatic growth parameters	Rhizobacteria having both 1-aminocyclopropane-1-carboxylate (ACC) deaminase and nitrogen fixing activity are more effective than rhizobacteria possessing either ACC-deaminase or nitrogen fixing activity alone for growth promotion of crops	Hassan et al. (2014)
Arbuscular mycorrhizal (AM) fungus *Rhizophagus irregularis* and *Variovorax paradoxus* 5C-2; Spain	Breeding and grafting techniques; growth responses and physiological mechanisms involved in the performance under drought stress of four tomato recombinant inbred lines	Inoculants affected plant parameters such as net photosynthetic capacity, oxidative damage to lipids, osmolyte accumulation, root hydraulic conductivity or aquaporin abundance and phosphorylation status.	Calvo-Polanco et al. (2016)
Pseudomonas chlororaphis and *P. extremorientalis*; Agricultural fields of Tashkent and Syr-Darya provinces	Pot experiment; Impact of PGPB plant growth and on the control of foot and root rot of tomatoes caused by *Fusarium solani* under different soil salinity conditions	Stimulated plant growth and acted as biological controls. The soil salinity did not negatively affect the beneficial impacts of PGPB, as they were able to colonize and survive under both saline and non saline soil conditions	Egamberdieva et al. (2017).

in significant reduction of productivity, yield and nutrients status (Tank and Saraf, 2010). Prolonged salinity stresses cause ions toxicity because of the increased concentrations of Na^+ and Cl^- ions. Such conditions induce oxidative stress by generating highly reactive oxygen species (ROS) such as singlet oxygen, hydrogen peroxide, hydroxyl radicals and superoxide, which are detrimental to cell viability (Meena et al., 2017). Therefore, PGPB mediated amelioration of low productive saline land sites may provide the chances for enhanced and better food production in order to minimize the food security problem for ever rising global population. It has been speculated that bacteria may protect plants against salt stress by modulation at physiological and biochemical levels (Glick, 2014). Available reports suggest that strategies for salt tolerance conferred by PGPB or endophytes mainly rely on altered plant root architecture which is regulated by hormones. Glick et al. (1998) have proposed a model suggesting ACC deaminase producing PGPB as a sink for ACC. Reduced ACC level either through endogenous or IAA stimulation results in reduction of ethylene content in plants. Hence, ACC deaminase producing PGPB can significantly reduce ethylene induced inhibition of plant growth following a wide range of stresses including salinity (Table 2) and drought (Table 3). Salinity induced stress in plants is partially a result of low level production of ethylene by plants, which may be overcome by secretion of ACC deaminase enzyme by PGPB thus protecting plants against this stress (Glick, 2014). Published reports have witnessed the role of ACC deaminase producing *Achromobacter piechaudii* ARV8 in enhancement of fresh and dry weight of tomato seedlings simultaneously with improved seedling survivability even at salt concentration up to 172 mM (Mayak et al., 2004a). This bacterium reduced the amount of ethylene production in seedlings of tomato, which was otherwise accelerated when seedlings treated with high salt concentrations. Although, the content of sodium in plant was not reduced, however, the uptake of phosphorus and potassium were slightly increased, which may play a key role in activation of

Table 3
An outline of drought management in tomato using PGPB.

PGPB and isolation sources	Experiments	Results	References
Achromobacter piechaudii ARV8; Sourthern Israel	Pot Experiment; isolation and molecular characterization using 16S rRNA; ethylene production analysis; RWC and WUE observation	Bacterium reduces ethylene production and increases WUE	Mayak et al. (2004b)
Azospirillum brasilense; Argentina	Nitric oxide quantification; seedling growth and lateral root measurement; bacterial colonization experiment	Nitric oxide induced lateral root and formation.	Creus et al. (2005)
Azospirillum brasilense Sp245, Argentina	Growth and NO production ability; evaluation of lateral root and adventitious root formation	Nitric Oxide as signaling molecule in lateral root and root hair formation	Molina-Favero et al. (2008)
Bacillus cereus AR156; China	Determination of relative water content, relative electrical conductance, antioxidant enzymes activity; expression of cytosolic ascorbate peroxidase, small subunit of Rubisco	Increased relative leaf water content, increment in chlorophyll a, chlorophyll b and total chlorophyll, marked increase in antioxidant enzymes	Wang et al. (2012)
Bacillus polymyxa; India	Determination of germination percentage, root length, shoot length, relative water content, proline, protein and chloroplyll content	Enhanced seed germination, root and shoot length, relative water content, yield	Shintu and Jayaram (2015)
Pseudomonas putida KT2440; Spain	Pot experiment in growth chamber; 16S rRNA gene sequencing; determination of root length, stem length, dry weight, fresh weight, and relative water content; trehalose production ability of bacteria; superoxide dismutase and catalase activity determination; production of IAA, GA and ABA	Protection from drought by production of plant hormone IAA, GA, ABA, trahalose and antioxidant enzymes	Vílchez et al. (2016)
Citrobacter freundii – J118; Pakistan	Pot experiment; characterization of ACC deaminase activity; Chitinase activity; siderophore production activity; Electrolytic leakage; RWC	Si and PGPB had great potential to alleviate drought stress and influenced tomato growth and yield, in addition to their effects on physiological characteristics and ionic relations.	Ullah et al. (2016)
Rhizophagus intraradices, Rhizophagus fasciculatum, and *Burkholderia seminalis*; India	Pot experiment; Determination of plant biomass, growth, and AMF colonization, Proline estimation, Guaiacol peroxidase activity determination	Significant increases in biomass, root length, shoot length, and chlorophyll content. Accumulation of proline was found to be less in AM fungi inoculated plants.	Tallapragada et al. (2016)

mechanisms involved during the alleviation of adverse effect of salinity on plant growth and development. The bacterium also increased the uptake capacity of water in saline environment and improved photosynthesis under elevated salt environment. Similar amelioration in plant growth is also reported by other workers (Ali et al., 2014; Hassan et al., 2014). Tank and Saraf (2010) reported reduced impact of salinity stress in plants by using PGPB inoculants that possessed plant growth promotion activity like phosphate solubilization, production of phytohormones, siderophores, and ACC deaminase enzyme even at 6% NaCl concentration. One of the bacterial isolate C4 was observed to improve the length of root and shoot by 50%. The study concluded that various PGPB isolates varied in mode of action against different levels of salinity stress. For example, C4 isolate inoculated plants were able to tolerate NaCl, due to lowered uptake of sodium chloride and thus reducing the effect of salt stress, while C5 isolate augmented the plant growth by enhancing the salt uptake and minimizing the concentration of salt in soil system.

4.2. Drought

Drought is also considered as one of the important abiotic stresses that negatively affects the growth and yield of crop plants cultivated mainly in the arid and semi-arid regions. Approximately, one third of world agricultural land is affected by drought stress, which poses severe threat to plant growth and food security (Yang et al., 2009). It has been speculated that by 2050 more than 50% of the arable lands will be affected by this severe problem (Kasim et al., 2013; Vinocur and Altman, 2005). In plants, drought environment can lead to oxidative stress because of increasing levels of reactive oxygen species (ROS), known to be responsible for imbalance of electron transport rates and metabolic consumer activity of reductive power (Beck et al., 2007). Plant tolerance to drought is mainly associated with the maintenance of plant water status either by reducing the loss or by improving water absorbing capacity through osmotic adjustment (Ullah et al., 2016). Generally, root systems acclimatize themselves to soil water deficiency by developing deep and extensive root systems for increased water extractions under drought condition. However, acclimation in such condition is assumed to affect the shoot growth and biomass resulting in various changes in physiological stages, such as seed germination and stem elongation during the initial stage of plant establishment (Yordanov et al., 2003). Reduced growth or leaf areas cause significant reduction in rate of photosynthesis which subsequently leads to decreased growth and yield of plants (Baligar et al., 2001). Altered biochemical response shows imbalance in electron transport mechanism due to induction of antioxidant defense system and reactive oxygen species (ROS) production (Vurukonda et al., 2016). Functional abnormalities are also associated with proteins denaturation caused by unfolding and dysfunction. Crop improvement using genetic manipulations are also being practiced to allow the expression of heat shock proteins (HSP) during stress condition (Wang et al., 2004; Vinocur and Altman, 2005). Several strategies have been suggested to overcome the negative impacts of drought stress in plants. However, few techniques such as plant breeding and genetic engineering for production of stress tolerant verities are tedious, expensive and time consuming process. Recently, researchers have made efforts to identify and exploit naturally inhabiting microbes to improve growth and yield enhancement of crops under changing climatic conditions (Nadeem et al., 2014; Yang et al., 2009). Although the role played by PGPB in growth promotion and disease management (Singh et al., 2017a,b; Kumar et al., 2017a,b) are well known, however, their performance in abiotic stress management including drought stress has recently gained more importance worldwide and needs more experimental trials before field level commercial application (Yang et al., 2009; Dimkpa et al., 2009; Grover et al., 2011). Implications of PGPB have also been found practical to overcome the drought effect on tomato plant. PGPB have been demonstrated to mitigate drought stress impact on plants through various mechanisms.

Rhizobacteria Induced Drought Endurance and Resilience (RIDER) is one of the common mechanism, which includes physiological and biochemical level changes in plants. The underlying physiological mechanisms include modification in levels of phytohormones, antioxidant defense systems, exopolysaccharides (EPS) production by bacteria, while those associated with metabolic adjustments encompasses accumulation of several organic solutes (like amino acids, sugars, and polyamines) as well as the production of dehydrins and volatile organic compounds (VOCs) (Ngumbai and Kloepper, 2016; Vílchez et al., 2016;

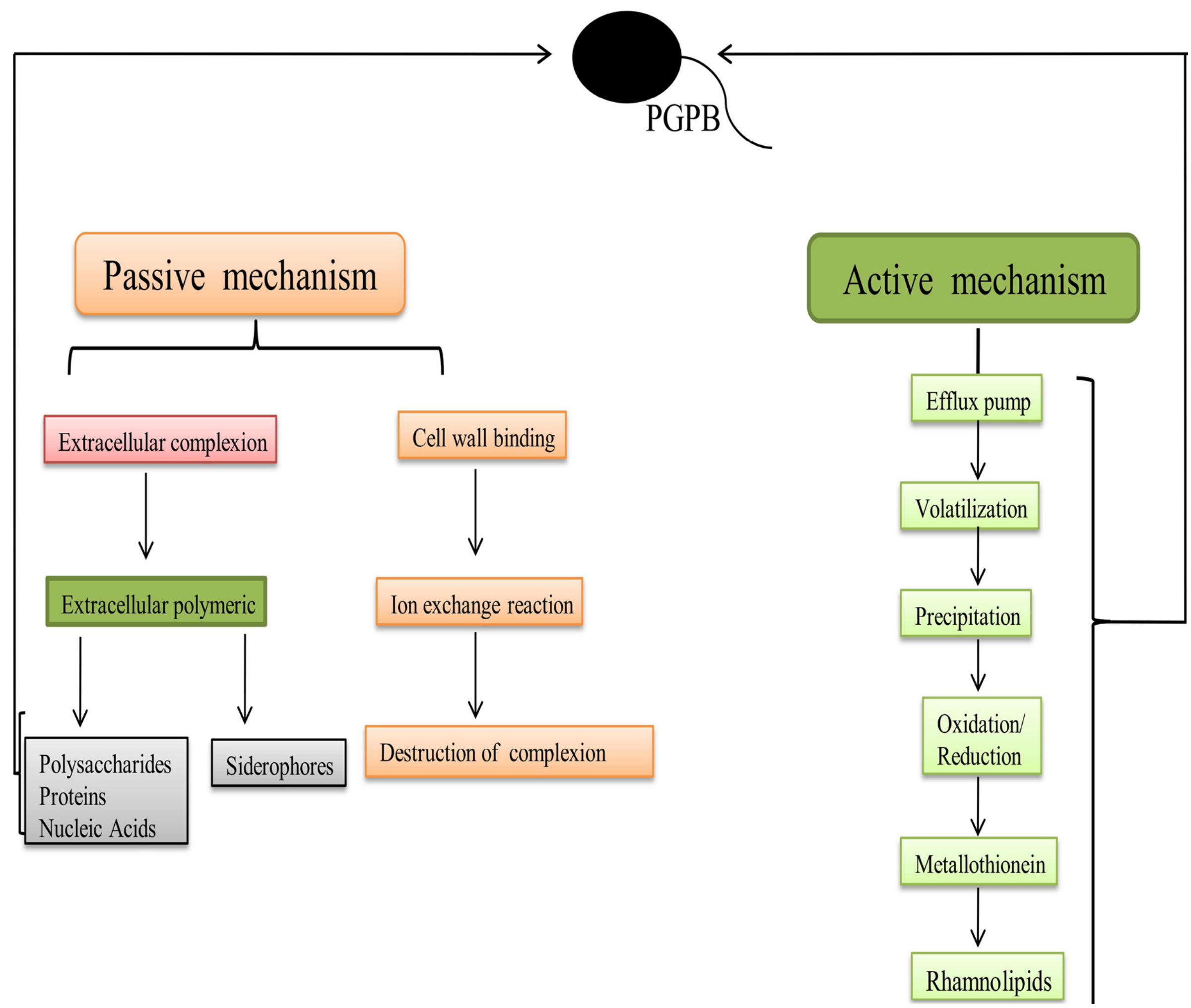

Fig. 3. An overview of heavy metal tolerance mechanism conferred by PGPB.

Kaushal and Wani, 2016a). The biochemical responses play significant role in drought tolerance. PGPB mediated amelioration of drought stress in tomato is primarily studied at the level of growth responses (Table 3). For instance, Juan et al. (2012) utilized plant growth promoting bacteria (PGPB) *Bacillus cereus* AR156 for enhancement of drought tolerance in tomato (*Solanum lycopersicum* L). Similarly, Ullah et al. (2016) found better results with combined application of Silicon and PGPB strain to alleviate negative effects of drought stress as compared to their individual application. Silicon and PGPB inoculation induced enhancement in K^{+}, Ca^{2+} and Mg^{2+} accumulation, relative water content and decrease in electrolyte leakage were the main factors associated with drought tolerance in tomato. Furthermore, some investigations have also reported the involvement of signal molecules in drought tolerance mechanisms in tomato. Few studies have acclaimed that bacteria like *Azospirillum brasilense* Sp245 possess nitric oxide synthase enzyme activity which is involved in stress tolerance and resistance. Nitric oxide (NO) is a mobile gaseous second messenger that is sensed at root level (Creus et al., 2005; Molina-Favero et al., 2008). However, still more field based experimental investigations should be conducted in order to reveal the PGPB mediated morphological and physiological responses such as root architecture modifications and drought tolerance.

4.3. Heavy metals

Heavy metal contamination of soil is also one of the prime concerns for agricultural soils because of their negative impact on crop productivity, human health and environment. Excess accumulation of heavy metals in the soil poses adverse effect on soil texture, crop productivity, growth, yield, nutrient availability, microbial community, and human health (Gupta et al., 2012; Etesami, 2018). High content of different heavy metals in soil not only affects the beneficial microbiological processes but also limits the crop yield by concentrating in different plant parts (Ahemad, 2012). High affinity ligands molecules present in plant enzymes and proteins chelate heavy metals effectively and reduce their toxicity. Interaction of heavy metals with plant protein and enzymes results into loss of their bioactivity which appears in form of chlorosis, stunted growth, root browning and loss of activity in photosynthetic apparatus (Shaw et al., 2004; Gorhe and Paszkowski, 2006). Presence of heavy metals in soil is also known to induce oxidative stress by producing reactive oxygen species (ROS) (Seth et al., 2008) which negatively affects the two important plant physiological processes *i.e.* photosynthesis and respiration causing overall reduction in plant productivity (Vangronsveld and Clijsters, 1994).

In case of tomato, higher concentration of Cd (1 and 10 μmol/L) significantly reduced the length and volume of root and height of tomato plant, whereas their lower concentration (0.1 μmol/L) slightly increased the plant height (Jing et al., 2005). In one study, focused on impact of Cd (1–10 μM) on antioxidative enzymes, it was concluded that high concentration significantly enhanced malondialdehyde (MDA) content, superoxide dismutase (SOD) and peroxidase (POD) activities causing oxidative stress responses in tomato (Dong et al., 2006). Furthermore, López-Millán et al. (2009) showed leaf chlorosis and necrotic spots on roots at 10 μM and 100 μM Cd concentrations,

respectively. Opeolu et al. (2010) reported reduced productivity of tomato without alteration in vitamin C content of tomato fruit when encountered with various concentrations (300, 600 and 1800 ppm) of $Pb(NO_3)_2$. Further studies revealed adverse effect of high concentrations of Pb on morphological and physiological parameters of tomato (Sędzik et al., 2015).

Bacterial cells respond to interacting heavy metals by various mechanisms such as sequestration into extracellular matrix, biosorption on cell wall, precipitation, oxido-reduction reactions, transport across the cell membrane and synthesis of metal binding protein (Jing et al., 2007; Singh et al. 2010). To acclimatize under metal stressed environment, soil inhabiting microbes including PGPB have evolved several mechanisms to escape the heavy metals (Fig. 3). Such metal tolerant/resistant PGPB possess quite environmental significance particularly in cases when they are utilized as bio-inoculant or biological fertilizers due to significant improvement in plant growth and development in heavy metal enriched/stressed soils. Field application of such bacteria having metal detoxification abilities along with plant beneficial attributes is an eco-friendly and low cost approach for metal remediation (Ahemad, 2014) as well as sustainable agriculture in metal contaminated soil.

For tomato few reports (Table 4) are available indicating the mitigation of heavy metal induced problems by using plant growth promoting bacteria (PGPB). Jiang et al. (2008) reported optimum antibiotic resistance and lead (Pb) and cadmium (Cd) toxicity removal by *Burkholderia* sp. J62 isolated from tomato rhizosphere. Madhaiyan et al. (2007) used *Methylobacterium oryzae* strain CBMB20 and *Burkholderia* sp. strain CBMB40 to reduce the toxicity of Ni and Cd in tomato. The inoculated bacteria promoted plant growth under gnotobiotic and pot culture experiments. Results showed that presence of PGPB strains significantly enhanced the growth of tomato in the presence of $NiCl_2$ and $CdCl_2$. In gnotobiotic assay, PGPB inoculation reduced the ethylene emission and increased the tolerance index of the seedlings against different concentrations of $NiCl_2/CdCl_2$ (Madhaiyan et al., 2007). Similar results were corroborated by Jing et al. (2005) and Dourado et al. (2013, 2014) who inoculated *Burkholderia* sp. in tomato plants under high concentration of Cd. Nemati and Bostani (2014) has also used microbial inoculants to mitigate the negative impact of elevated concentration of Cd and Pb. In another study, He et al. (2009) used strains of *Pseudomonas* and *Bacillus* in order to manage the load of soil heavy metals such as Cd and Pb. They revealed that inoculation of PGPB significantly enhanced the root length of treated tomato seedlings as compared to control. Garcia-Lopez and Delgado (2016) used *Bacillus* QST713 strain to examine the impact of higher concentration of phosphate and Fe oxide (ferrihydrite) on growth of tomato and cucumber. They found that PGPB inoculated with strain QST713 increased overall plant growth and total plant phosphorus by 40%. Burd et al. (1998, 2000) used plant growth promoting bacterium, *Kluyvera ascorbata* SUD165 and a siderophore overproducing mutant *K. ascorbata* SUD165/26 to protect the plants against inhibitory effects of high concentrations of nickel, lead, and zinc. The ameliorating effect of PGPB was attributed to sufficient supply of iron to plant.

5. PGPB mediated remediation of contaminated sites

Over past few decades, remediation of polluted sites has become a prime concern for researchers as well as government also, because rapid industrializations have exacerbated the release of anthropogenic chemicals into the environment. These commonly occurring contaminants include heavy metals, petroleum hydrocarbons (PHCs), polycyclic aromatic hydrocarbons (PAHs), halogenated hydrocarbons, pesticides etc. The negative impacts of these pollutants on the environment and on human health are well documented by different researchers (Gerhardt et al., 2009). Currently, various technologies of physical and chemical

Table 4
An overview of PGPB mediated heavy metal tolerance mechanism in tomato.

PGPB and isolation sources	Experiments	Results	References
Burkholderia sp. J62; China	Pot experiment; isolation and molecular characterization using 16S rRNA; heavy metal- and antibiotic resistance and heavy metal solubilization assays; plant growth promoting characters evaluation	Bacterium showed high degree of resistance to different antibiotics and heavy metals. Especially to Pb and Cd, it causes their solubilization in solution culture and soils making their availability to increase from 38% to 192% and 5% to 191%, respectively in inoculated plant tissues with significant ($p < 0.05$) increase in the biomass of maize and tomato plants	Jiang et al. (2008)
Pseudomonas fluorescens G10 and *Microbacterium* sp. G16; China	Pot experiment; isolation and molecular characterization using 16S rRNA; heavy metal- and antibiotic resistance and heavy metal solubilization assays; root elongation assay	Bacterium showed high degree of resistance to different antibiotics and heavy metals; significantly ($p < 0.05$) increased water-solubility of Pb in solution and in Pb added soil. Root elongation assays demonstrated increases in root elongation.	Sheng et al. (2008)
Burkholderia sp. SCMS54; Brazil	Isolation and molecular characterization using 16S rRNA; plant–bacteria interaction bioassay	Bacterium provided tolerance to Cd by decreasing plant peroxide and chlorosis levels (global stress response); promoted relative plant growth and decreased Cd absorption via beneficial interaction with the roots.	Dourado et al. (2013)
Kluyvera ascorbata SUD165 and *K. ascorbate* SUD165/26; Ontario	Pot experiment; isolation based on selective medium growth; siderophore assay; protein assay; chlorophyll assay; ACC deaminase determination	Bacteria exhibited pronounced effects on plant growth promotion and protection against the inhibitory effects of high concentrations of Ni, Pb, and Zn by providing sufficient amount of iron to the plants	Burd et al. (2000)
Methylobacterium oryzae strain CBMB20 and *Burkholderia* sp. strain CBMB40; Republic of Korea	Pot experiment; isolation; gnotobiotic assays; heavy metal tolerance assay	Bacteria rendered protection against the heavy metal (Ni, Cd) toxicity by reducing their uptake and further translocation to shoots in plants and promoted the plant growth	Madhaiyan et al. (2007)
Pseudomonas sp. RJ10 and *Bacillus* sp. RJ16; China	Pot experiment; isolation; root elongation assay; heavy metal tolerance assay	Bacteria rendered high degree of resistance to heavy metals (Cd, Pb) making their $CaCl_2$-extractable content to increase from 58 to 104% and 67 to 93%, respectively in heavy metal contaminated soil	He et al. (2009)
Baillus QST713 strain; Spain	Cylindrical pot; plant P uptake from variable P compounds i) P source (KH_2PO_4 at 100 mg kg^{-1}, and phosphate rock [PR] at 100 or 200 mg kg^{-1}); (ii) plant inoculation with QST713	Inoculation with QST713 increased plant growth and total accumulation of P by 40%. Higher concentration of ferrihydrite decreased dry matter yield in plants by more than 50 %	Garcia-Lopez and Delgado (2016)

nature exist for management of contaminated sites. Several limitations are known to prevail while employing the physico-chemical practices for remediation of contaminated sites. Biological treatment techniques on the other hand, being eco-friendly in nature are much attractive, less expensive and suitable choice for phytoremediation. Although, phytoremediation and bioaugmentation/ bioremediation processes are quiet popular; however, certain factors such as nutrient poor soil or bioavailability of contaminant impedes the rate of remediation (Siciliano et al., 2003). Several reports witnessed the degradation of large recalcitrant organic compounds by the rhizosphere associated microbes, referred as rhizoremediation (Schwab and Banks, 1994). Bisht et al. (2015) has critically reviewed the importance of remediation ability of several microbes for polyaromatic hydrocarbons (PAHs) contaminated sites. Most of the potent microbes are reported from contaminated sites; however, such microorganisms are also reported from non contaminated sites. Tesar et al. (2002) have successfully demonstrated the ability of rhizospheric bacteria associated with poplar and some herbal plants to clean the diesel contaminated sites. Grass inoculation with *Pseudomonas aeruginosa* strain R75 has been shown to stimulate the seed germination by 80% and 2-Chlorobenzoic acid (2-CBA) degradation upto 20% (Siciliano and Germida, 1997). *Elymus dauricus* association with *Pseudomonas savastanoi* and *Pseudomonas aeruginosa* enhanced the 2-CBA degradation by 112% as compared to unioculated control. Rhizoremediation is the inherent coordination of interactions involving roots, root exudates and rhizospheric microbes resulting in degradation of even complex organic compounds. The process of rhizoremediation practice largely depends on the bacterial root colonization efficiency which further relies on chemotaxis and may be accelerated by applying certain elicitors (Weert et al., 2002). Death and decay of root cap cells or even entire root causes release of nutrients to favor the growth of rhizospheric bacteria (Lugtenberg and de Weger, 1992). Furthermore, role and importance of PGPB producing ACC deaminase in rhizoremedation, has opened the door for root modification that may accelerate the degradation capacity in both field and/or lab conditions (Glick, 2014). *Pseudomonas* demonstrates effective chemotactic response towards the malic acid, citric acid, and amino acids (especially leucine) that help in colonization of tomato roots (Weert et al., 2002; Oku et al., 2012), while rhizosphere associated species of *Burkholderia* have shown the potential to degrade organic contaminants (Mellado et al., 2007).

Development of heavy metal tolerant crops through genetic engineering technology is tedious and expensive process while mitigation through PGPB inoculation technology is cost effective, sustainable and eco-friendly approach for management of heavy metals and organic contaminants affected land areas. Therefore, collaborative future research requires the identification of the potential microbes and their proper field evaluation in sustainable agricultural perspectives.

Very limited data are available regarding the rhizoremediation potential of tomato associated microbes. Knowing and suitably altering the rhizospheric biology of tomato can help a lot in management of diseases, crop productivity, soil management and remediation of contaminated sites. Opting PGPB for rhizoremediation is attractive because of simultaneous growth promotion as well as *in situ* remediation of contaminated sites. PGPB assisted inorganic and organic contaminant removal have been reported in many plant species including sugar beet, barley, wheat, poplar, oat, radish, corn, astragalus and lupin (Kuiper et al., 2004). The PGPB being employed for rhizoremediation must possess the characteristics such as pollutant tolerance, efficient root colonization, competence against the non-rhizospheric microbe by siderophore production or phosphate solubilzation.

6. Future prospective

Since decades, PGPB has been enhancing the agriculture productivity through different mechanisms and processes. However, there is variability in performance of PGPB that may be due to various environmental factors that might affect the growth and proliferation of plants growing under natural environmental condition. With the introduction of modern approaches and techniques, such as micro-encapsulation and nano-encapsulation in the field of agro-biotechnology and nanotechnology, the agriculture sector has acquired a boost during the recent decades. The unique size dependent properties of nano-materials make them superior and indispensable in many areas of sustainable agriculture development. Moreover, genetic manipulation or transformation can be employed to develop effective PGPB strains that can work best even at low inoculum dose and survive under a wide variety and range of harsh environmental conditions. Therefore, it is imperative to develop more potent PGPB strains with longer shelf-lives to achieve sustainable crop production under given environmental stress. Apparently, PGPB confer tolerance to plants against certain stress conditions by modulating the level of various essential enzymes. Ethylene is one of the most important plant hormone that mediates response to variety of stressors. It is generally hypothesized that production of ethylene beyond the threshold level act as “stress ethylene” which is unfavorable for plants growth and development. PGPB are known to modulate the synthesis and production of some specific enzymes, which provoke physiological changes in plants at molecular level. Among these enzymes, bacterial ACC deaminase plays a key role in regulation of hormone like ethylene, which regulates the growth and development of plants under salinity and drought stress. Bacterial strains harboring ACC deaminase activity can alleviate the stress induced ethylene mediated negative impact on plants. Therefore, agricultural crops confronting stress conditions can be genetically improved by incorporation of genes encoding ACC deaminase using molecular techniques like genetic engineering. Such techniques can be extended for developing ACC deaminase over expressing microbes. Furthermore, identification of rhizosphere associated microbial interaction is now becoming the prime research area and can be regarded as the frontier in the sustainable agriculture. Use of next generation sequencing like throughput techniques may reveal functional aspects of the interactions at community level. Such studies can be utilized to identify the fate and types of microbes present in different environmental stress conditions. Bioremediation has emerged as a potential tool to clean up the metal contaminated/polluted environment. Reducing the bioavailability of metal contaminants in the rhizosphere (phytostabilization) as well as improving plant establishment, growth, and health could significantly speed up the plant growth and indeed its productivity (Ma et al., 2011). Moreover, currently very scanty reports are present to analyze, how the root exudates of plant interact and regulate the microbial population and diversity; knowledge is lacking on these interactions especially at the community level and also how these rhizospheric microbial communities influence composition of root exudates? Multi-omics approaches including genomics, transcriptomics, proteomics, and metabolomics can help to bridge the knowledge gap of interactions and coevolution of microbes with plants under extreme abiotic environments. Also, this will help to produce multi-layered information that may solve the problems of what is happening exactly within the interacting components of bacteria and other microbes in rhizosphere.

Conflict of interest

Authors declare no conflict of interest.

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